CONTRIBUTIONS FROM THE ZOÖLOGICAL LABORATORY OF THE MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD COLLEGE. E. L. MARK, DIRECTOR. No. 117.

STUDIES ON THE CAUSE OF THE ACCELERATING EFFECT OF HEAT UPON GROWTH.

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THE following studies, directed toward a further analysis of the fact that the rate of growth of organisms varies with temperature, were made at the suggestion and with the guidance of Dr. C. B. Davenport. Growth, defined as increase in volume or mass, is evidently produced by one or both of the following processes: either (1) by imbibition of water, which results in an increase of cell sap, or (2) by assimilation, *i.e.*, anabolic metabolism, which results in the increase of plasma and of formed substance, such as starch, cellulose, etc. The question to which an answer was sought is this: In the acceleration of growth due to higher temperature, are imbibition of water and anabolic metabolism equally accelerated? or, if unequally affected, in which process is acceleration most marked?

The procedure embraced the following points:

1. Experiments were made upon the larvæ of *Rana sylvestris*, *Amblystoma punctatum*, and *Bufo americana*.

2. Fertilized eggs of a single spawning were subjected to three different temperature conditions: (1) 6°–8° C., (2) 12°–18° C. (12°–15° C. in Rana), and (3) 22°–25° C. (20°–24° C. in Amblystoma). The other conditions were as nearly as possible alike in the three cases.

3. No food was supplied other than that contained in the egg and in the albumen surrounding the embryo; consequently, these results apply only to the early stages of development in the amphibian embryo.

TABLE I. — RANA SYLVESTRIS.

DATE.	No. of Days.	Length. mm.	Average Weight. mg.	Av. Wt. Dry Substance. mg.	Average Weight Water. mg.	Per cent of Dry to Whole Weight.
	1. TEMPERATURE 6°–8° C.					
March 23[1] . . .	—	—	3.98	1.50	2.48	37.5
April 5	13	5	4.46	1.49	2.97	33.4
" 8	16	6	5.04	1.58	3.46	31.3
" 11	19	7.5	6.12	1.64	4.48	26.8
" 16	24	10	8.26	1.58	6.68	19.1
" 19	27	10	9.50	1.54	7.96	16.2
" 22	30	10.7	10.12	1.50	8.62	14.8
" 27	35	11.2	13.30	1.44	11.86	10.9
" 29	37	12	12.70	1.40	11.30	11
May 3	41	12.2	19.10	1.44	17.66	7.5
" 5	43	12.2	19.38	1.44	17.94	7.4
" 12	50	13.5	21.02	1.52	19.50	7.2
	2. TEMPERATURE 12°–15° C.					
March 23[1] . . .	—	—	3.98	1.50	2.48	37.5
" 29	6	7	6.66	1.62	5.04	24.3
" 30	7	8	7.06	1.50	5.56	21
April 1	9	10.5	10.49	1.51	8.98	14.3
" 4	12	12.5	18.32	1.46	16.86	8
" 6	14	13.5	22.60	1.30	21.30	5.7
" 8	16	14.5	28.18	1.78	26.40	6
" 12	20	16	36.30	1.70	34.60	4.7
" 16	24	16.5	37.96	1.82	36.14	4.7
" 20	28	17	39.82	1.98	37.84	4.4
" 22	30	17	33.50	1.76	31.74	5.2
	3. TEMPERATURE 22°–25° C.					
March 23[1] . . .	—	—	3.98	1.50	2.48	37.5
" 25	2	11	5.29	1.30	3.99	24.6
" 29	6	19	18.01	1.18	16.83	6.5
April 1	9	—	24.56	1.25	23.31	5.1
4. INDIVIDUALS OF SAME SPAWNING TAKEN FROM 2 (SEE "MARCH 30" ABOVE), AND PLACED IN 3, AFTER THEY HAD BEEN IN AQUARIUM 7 DAYS.						
March 30	7	8	7.06	1.50	5.56	21
" 31	8	11	10.28	1.32	8.86	12.8
April 1	9	13	17.10	1.30	15.60	8.8
" 4	12	14	25.23	1.43	24.80	5.7
" 6	14	14.5	35.62	1.42	34.10	4
" 8	16	14.5	36.02	1.41	34.61	3.9
" 12	20	14.5	32.16	1.35	30.81	4.2

[1] Weight of embryo free of albumen, at beginning of experiment, several days before hatching.

4. The measurements taken were: (1) maximum length, (2) total weight when freed of superficial water, and (3) dry weight, obtained by desiccating the animals in an air-tight chamber containing sulphuric acid until they ceased to lose

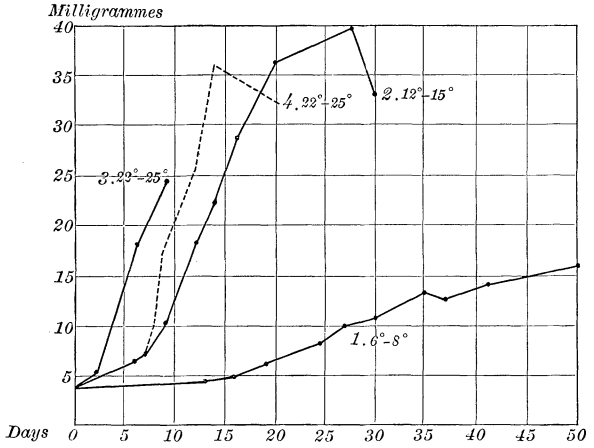

FIG. 1. — Rana. Graphic representation of Table I, column 4, showing average total weight on successive days of the experiment.

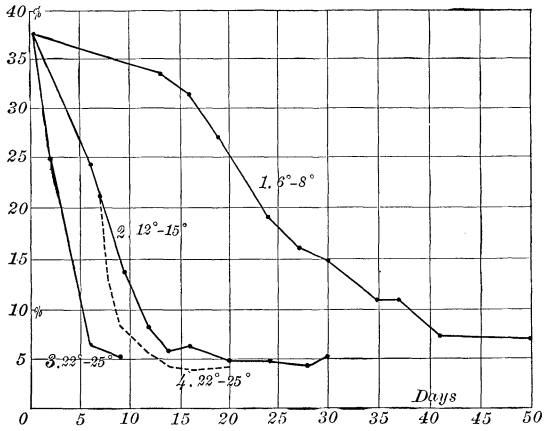

FIG. 2. — Rana. Graphic representation of the ratio of dry substance to the total weight. (See Table I, column 7.)

weight. From these were derived the amount of water present and the percentage of dry substance.

5. *Five* individuals were taken at random in determining all the averages recorded in this paper, except in the later

TABLE II. — AMBLYSTOMA PUNCTATUM.

DATE.	No. of Days.	Length. mm.	Average Weight. mg.	Av. Wt. Dry Substance. mg.	Average Weight Water. mg.	Per cent Dry Substance.
1. TEMPERATURE 6°–8° C.						
April 12	—	—	—	—	—	—
" 22	10	7.5	6.82	3.02	3.80	44.2
" 27	15	8.5	8.62	2.92	5.70	33.8
May 7	25	10	9.54	2.58	6.95	27
" 17	35	12	13.70	2.70	11.00	19.7
" 24	42	13	16.22	2.70	13.52	16.6
" 26	44	13.5	17.46	2.68	14.58	15.3
June 2	51	14	19.20	2.66	16.54	13.8
" 6	55	14.5	23.80	2.64	21.16	11.1
" 10	59	15	25.82	2.46	23.36	9.5
" 20	69	16	29.64	2.24	27.40	7.5
2. TEMPERATURE 12°–18° C.						
April 12	—	—	—	—	—	—
" 20	8	9	9.94	2.90	7.04	29.1
" 27	15	12	12.26	2.74	9.52	22.3
" 29	17	13	15.00	2.84	12.16	18.9
May 3	21	14	18.52	2.64	15.88	14.2
" 7	25	15	22.92	1.88	21.04	8.2
" 17	35	16.5	28.40	2.32	26.08	8.1
" 20	38	16	24.08	1.88	22.20	7.8
" 24	42	17	26.70	2.02	24.68	7.6
" 28	46	17	23.60	1.50	22.10	6.3
3. TEMPERATURE 20°–24° C.						
April 12	—	—	—	—	—	—
" 16	4	8.5	8.79	2.69	6.10	30.6
" 20	8	10.5	9.78	2.68	7.10	27
" 22	10	12	12.20	2.59	9.61	21.2
" 25	13	14	14.64	2.78	11.86	19
" 29	17	14	21.84	2.58	19.26	11.8
May 3	21	14.7	23.94	2.22	21.72	9.2
" 7	25	15	22.78	2.54	20.24	11.1
" 16[1]	34	14.5	17.80	1.86	15.94	10.4
" 20[1]	38	14.5	17.00	1.20	15.80	7

[1] Good many dying; evidently not thriving.

measurements of Bufo at the highest temperature; in this latter case *three* were taken.

Results. — The results are embodied in the accompanying tables and in the curves (Figs. 1–6) constructed from them.

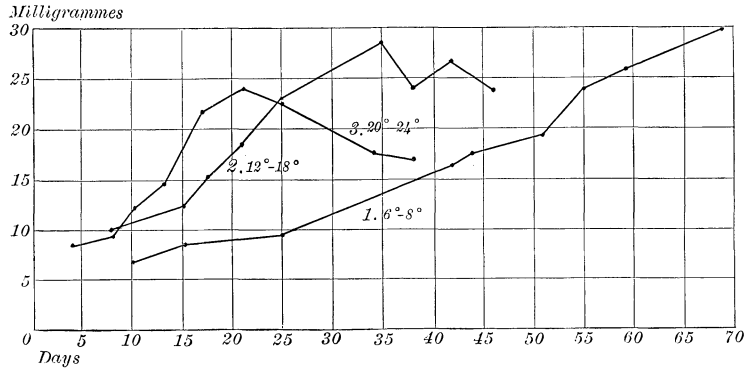

FIG. 3. — Amblystoma. Graphic representation of Table II, column 4, showing average total weight on successive days of the experiment.

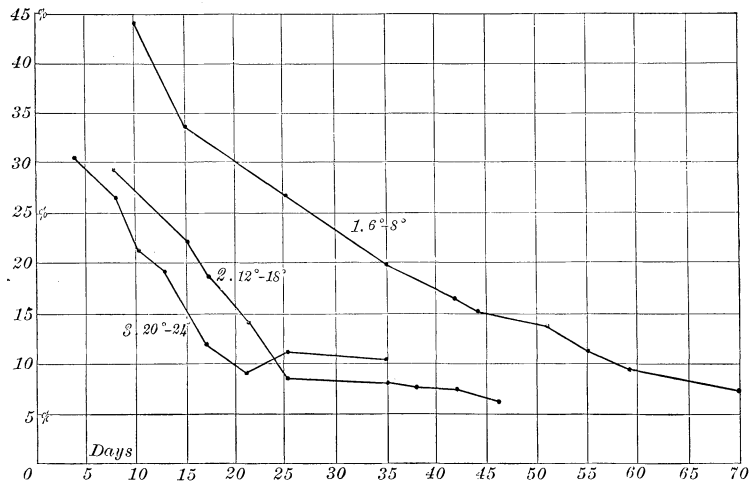

FIG. 4. — Amblystoma. Graphic representation of the ratio of dry substance to the total weight. (See Table II, column 7.)

The column headed "No. of Days" indicates the number of days reckoned from the beginning of the experiment, — not from hatching. The exact date of fertilization is unknown.

In Table I it will be seen that there are two sets of observations

recorded for the highest temperature. Owing to great acceleration and high rate of mortality, the first series (I; 3) was very short. To supplement this record I took some embryos of the same spawning, which had been for seven days in the aquarium, at a temperature of 12°–15° C., and placed them in the warm chamber (I; 4).

An accident prevented my getting a record for Bufo at the lowest temperature (6°–8° C.).

Conclusions. — 1. All the processes involved in the early development of these larvæ are accelerated by an increase of

TABLE III. — BUFO AMERICANUS.

DATE.	*No. of Days.*	*Length. mm.*	*Average Weight. mg.*	*Av. Wt. Dry Substance. mg.*	*Average Weight Water. mg.*	*Per cent Dry Substance.*
1. TEMPERATURE 12°–18° C.						
April 26	—	—	—	—	—	—
May 3	7	4.8	3.00	.82	2.18	27.3
" 5	9	6	3.36	1.02	2.34	30
" 7	11	7.5	5.98	.98	5.00	16.3
" 17	21	10.5	12.68	.84	11.84	6.6
" 20	24	10.5	11.00	.70	10.30	6.4
" 24	28	10.8	12.00	.64	11.36	5.3
" 28	32	10.5	12.08	.51	11.57	4.2
" 31	35	10.5	11.62	.60	11.02	5.1
2. TEMPERATURE 22°–25° C.						
April 26	—	—	—	—	—	—
" 30	4	5	2.50	.86	1.64	34.4
May 2	6	8	4.40	.94	3.46	21.4
" 3	7	10	9.54	1.10	8.44	11.5
" 5	9	11	15.96	1.00	14.96	6.6
" 7	11	13	21.00	.96	20.04	4.6
" 9	13	13	21.44	.92	20.52	4.3
" 10	14	13	22.12	.90	21.32	4
" 17	21	13	20.82	1.01	19.81	4.8

temperature within the limits used: + 6° to + 25° C. This is true of the early cell divisions preliminary to hatching, as

well as of the beginning and ending of the period of rapid imbibition of water.

2. Under the conditions of the experiment, the absolute dry weight appears to undergo little change. There is apparently a slight loss from the beginning of the experiment to the period of maximum percentage of water in the embryo. In studying the data I do not find any constant relation between this decrement and the temperature. Inasmuch as the prevailing difference in dry weight is so slight, it seems probable that the sudden fluctuations of weight seen in some of the measurements may be due partly to individual variation in the amount of food taken and in the presence of fæcal matter in the digestive tract, and partly to errors in weighing, which may amount to as much as 0.5 milligram. In some of the smaller weighings this would mean a possible error of 20%. Of course the *probable* error is much less than this. It appears safe to say that during the period embraced in my experiments, — from hatching until the attainment of the maximum percentage of water, — the dry weight is *unaffected* by temperature. It follows, therefore, that the acceleration and retardation experienced at this period in the growth of the larvæ by reason of different temperature conditions is due almost entirely to the changed rate of imbibition of water.

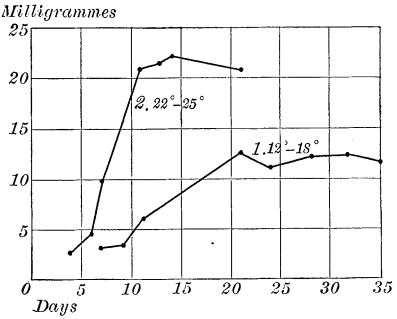

FIG. 5. — Bufo. Graphic representation of Table III, column 4, showing average total weight on successive days of experiment.

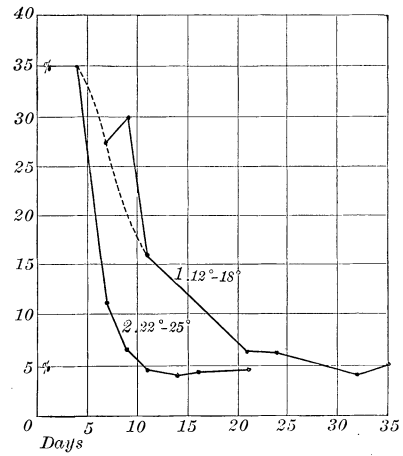

FIG. 6. — Bufo. Graphic representation of the ratio of dry substance to the total weight. (See Table III, column 7.) The broken line indicates the probable position of the curve; the second measurement is doubtless inaccurate.

3. The measurements of Rana also show that there was no appreciable gain in the dry weight of the egg, with the albumen removed, *up to the time of hatching*. There was during the same time a slight increase of water. Thus it appears that a part of the acceleration — by increased temperature — of the cell multiplications leading up to hatching may be due to the earlier inauguration of the imbibitory process.

4. The developmental process up to the point where the water amounts to 75% of the whole weight is not retarded so much by lowered temperature as is the stage representing the *maximum* percentage of water (see Table IV). In the first stage assimilation of yolk and cell division is prominent; in the latter imbibition of water is the main process. The

TABLE IV. — DESIGNED TO SHOW RELATIVE RETARDATION OF AN EARLY AND A LATER EVENT IN THE LARVAL DEVELOPMENT, PRODUCED BY LOWER TEMPERATURES.

	1. TIME IN DAYS REQUIRED TO ATTAIN 75% OF WATER; *i.e.*, 25% DRY SUBSTANCE.			2. TIME IN DAYS REQUIRED TO ATTAIN MAXIMUM PERCENTAGE OF WATER.		
	Highest Temperature.	*Medium Temperature.*	*Lowest Temperature.*	*Highest Temperature.*	*Medium Temperature.*	*Lowest Temperature.*
Rana	2	5.7	20	5	28	50 +
Amblystoma	9	12	27	21	50 +	70 +
Bufo	5.5	7.5	—	14	32	—
Average	5.5	8.4	23.5	13.3	36.6	60 + [1]
Retardation in days, reckoned from time required by highest temperature	—	2.9	18	—	23.3	46.6 +
Retardation in per cent	—	53%	327%	—	175%	350% [1]

[1] This result is certainly too small, since the length of time consumed in my observations did not suffice to reach the minimum percentage of dry substance in the lowest temperature conditions.

conclusion reached above (2), *viz.*, that it is chiefly the imbibitory process which is accelerated by heat, is thus further strengthened.

5. Organisms reared in the warmer conditions tend to attain a maximum percentage of water *slightly higher* than that reached by those reared at a lower temperature. This fact accentuates the conclusion reached in 4, in that a shorter time is required to accomplish a greater result.

6. On the other hand, it appears (see Figs. 1 and 3) that the lower temperatures allow the attainment of a somewhat greater *maximum total weight*, no extraneous food being supplied. The significance of this is not apparent. It is possibly due to the albuminous food material in the egg envelope being better preserved, and hence more completely available as food after hatching, than at the higher temperatures.

7. Finally, the individuals which were subjected for seven days to a temperature of 12°–15° and were then placed in a warm chamber, showed a greater rate of increase of imbibition water than those reared in the warm chamber from the beginning (Figs. 1 and 2). This indicates a tendency compensatory for early unfavorable circumstances, — an instance of the well-known regulative capacity of organisms.